CAULIFLOWER, A NEW RECESSIVE MUTATION IN TOMATO[1]

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A new, apparently mendelian recessive character, here proposed to be known as cauliflower, first came to the attention of the writers in a field planting of F_2 tomatoes at Wooster, Ohio, in 1949. As far as the writers have been able to ascertain this mutant has not been previously observed or reported. On those plants where the character is found, each individual inflorescence is of the cauliflower type (fig. 1). Plants which produce cauliflower type inflorescences in the field also produce them when grown under glass. The earliest inflorescence primordia visible to the naked eye are already abnormal and resemble a head of cauliflower. The inflorescence stem system is multibifurcated. This abnormality apparently begins extremely early in development (fig. 2). The bifurcations are not exactly equal and the inequality alternates from side to side at successive branches with the result that in old inflorescences a main axis can be traced. The smaller branches seem to arise in the axil of a filiform bract in the younger portions of old inflorescences.

The structure found where each flower should be is actually a growing point. This is evident because the inflorescence becomes progressively larger and more bifurcated as the season advances. Some inflorescences reach a size of 12 inches across, and feel very much like a large sponge when grasped. The growing points are not enclosed by leaf or scale primordia (figure 2). In some instances, normal leafy stem growth has come from a cauliflower inflorescence. However, all inflorescences on the internodes of the resumed growth are of the cauliflower type (fig. 3).

Cauliflower is similar to complex (*ss* genotype) in that both are multibifurcate. They differ in that cauliflower is more extensively bifurcated and in that a flower never has been seen to arise on a cauliflower type inflorescence (fig. 4).

The plants which originally produced the cauliflower type inflorescence were observed in three field plots each of which had been planted from the seeds of a single fruit. All three fruits had come from the same F_1 individual. Cauliflower-producing plants occurred in approximately a 3: 1 ratio (tables 1 and 2). No

TABLE 1

Pedigree of progenies in which the new cauliflower type of inflorescence has appeared.

P_1	P. I. 148720 (Baldwin's Brazilian)	× P. I. 79532 (Missouri Accession 160)
F_1	7 plants, all normal 7 selfed	
F_2	6 did not segregate 1 segregated (162 normal: 70 cauliflower) 30 from one field plot of the segregating progeny selfed	
F_3	13 did not segregate 17 segregated (365 normal: 106 cauliflower) 33 from two of the segregating progenies selfed	
F_4	11 did not segregate 22 segregated (419 normal: 148 cauliflower) 7 from one segregating progeny selfed	
F_5	2 did not segregate 5 segregated (84 normal: 16 cauliflower)	

[1]Experiment Station Journal Article 31.

TABLE 2

Frequency of cauliflower inflorescence producing plants in F_2, F_3, F_4, and F_5 generations.

GENERATION TESTED		NUMBER PLANTS NORMAL	NUMBER PLANTS CAULIFLOWER INFLORESCENCE	TOTALS	TOTALS χ^2	TOTALS df	TOTALS P	HETEROGENEITY χ^2	HETEROGENEITY df	HETEROGENEITY P
F_2 Generation—6 samples from single F_1 plant.										
Totals of 3 Fusarium inoculated samples	Observed	96	40	136	1.412	1	0.30–0.20	0.102	2	0.98–0.95
	Expected	102	34							
Totals of 3 uninoculated samples	Observed	66	30	96	2.000	1	0.20–0.10	1.932	5	0.50–0.30
	Expected	72	24							
Total observed		162	70	232	3.372	1	0.10–0.05	2.074	5	0.95–0.70
F_3 Generation—17 segregating progenies.										
Totals of 12 Fusarium inoculated progenies	Observed	288	75	363	3.644	1	0.10–0.05	10.240	11	0.70–0.50
	Expected	272	91							
Totals of 5 uninoculated progenies	Observed	77	31	108	0.790	1	0.50–0.30	2.461	4	0.70–0.50
	Expected	81	27							
Total observed		365	106	471	2.608	1	0.20–0.10	14.527	16	0.70–0.50
F_4Generation—22 segregating progenies.										
Totals of 22 uninoculated progenies	Observed	419	148	567	0.368	1	0.70–0.50	22.326	21	0.50–0.30
	Expected	425	142							
F_5 Generation—5 segregating progenies.										
Totals of 5 uninoculated progenies	Observed	84	16	100	4.320	1	0.05–0.02	0.591	4	0.98–0.95
	Expected	75	25							
Hybridizations of known heterozygotes—12 progenies.										
Totals of 12 uninoculated progenies	Observed	420	154	574	1.024	1	0.50–0.30	4.826	11	0.95–0.90
	Expected	430	144							
Totals for all 62 tested progenies.										
Totals	Observed	1450	494	1944	0.176	1	0.70–0.50	55.860	61	0.70–0.50
	Expected	1458	486							

cauliflower plants appeared among 28 field plots from single fruits of six sister F_1 individuals of the same cross. It therefore seems likely that the actual mutation occurred early in the ontogeny of this one particular F_1 plant. The original cross had been made between P.I. 148720 (designated Baldwin's Brazilian) as female parent and P.I. 79532 (known as Missouri Accession 160) for the purpose of studying the linkage relationships of the Fusarium immunity locus *I/i*. Consequently, the F_2, in which the mutation became homozygous, was composed entirely of plants which had survived a severe Fusarium inoculation and presumably were either *II* or *Ii* in genotype.

To determine whether the Fusarium inoculation had affected the observed ratio of cauliflower versus non-cauliflower, another planting of each of the three seed remnants was made and uninoculated plants were classified (table 2). Again the deviations from a 3: 1 ratio are not significant. Thus, there is no apparent effect on the segregation of cauliflower attributable to Fusarium inoculation. It may therefore be presumed that the *I/i* and cauliflower loci are not linked.

Seed was harvested at the end of the 1949 season from each of 30 of the 31 non-cauliflower Fusarium inoculation survivors present in one of the three progenies. Seeds from 13 of these were planted for the F_3 generation in the greenhouse during the ensuing winter without being subjected to Fusarium inoculation. Seeds from the other 17 were not planted until the following spring. These latter 17 progenies were subjected to a Fusarium inoculation and raised in the field. The choice of the first 13 was made by using the seed from the first 13 consecutive normal plants in the field plot.

If cauliflower is inherited as a simple mendelian recessive, not linked with *I/i*, two-thirds of these 30 progenies should have segregated and in each such progeny the segregation should have approximated a 3: 1 ratio. Segregation did occur in five of the non-inoculated progenies and in 12 of the inoculated progenies (tables 1 and 2). The heterogeneity χ^2 for these two ratios of 5: 8 and 12: 5 is 3.774 with 1 degree of freedom and P is 0.10–0.05. This heterogeneity is undoubtedly spuriously large because among the 13 non-inoculated progenies, there were five non-segregators in which there were fewer than 16 plants each. Some of these five might have proved to be segregators if greater numbers of F_3 offspring could have been raised. Even so, the above χ^2 is not significant and it is permissible to treat all 30 tested progenies as a single sample of 17 segregators to 13 non-segregators. The χ^2 for the deviation of 17: 13 from the expected 2: 1 is 1.350 with 1 degree of freedom and P is 0.30–0.20. Here again, the χ^2 is probably spuriously large for the same reason as above.

The same 30 progenies were also classified for stem hairiness. The F_2 generation had been also so classified. The F_3 generation was classified as a check on the classification of the F_2 generation. Five of the 30 F_2 individuals had been classified as hairy (*hh* genotype). These five F_2 individuals produced only hairy individuals in the F_3 generation. No other F_3 progeny was composed entirely of hairy plants. In other words, in all 30 instances the direct F_2 classification was confirmed by the F_3 progeny test. The F_3 generation data in addition made it possible to distinguish between *HH* and *Hh* among the 25 non-hairy F_2 individuals. The frequencies of the six possible combinations of cauliflower genotype and stem hairiness genotype thus found among these 30 F_2 individuals are summarized in table 3. None of the χ^2 values are significant when testing the expectation of 1: 2: 1: 2: 4: 2 ratio. There is thus no basis for presuming linkage between the *H/h* and cauliflower loci. In table 3 the 17 Fusarium inoculated progenies are presented separately from the 13 non-inoculated progenies. The heterogeneity χ^2 reveals that the Fusarium inoculation apparently had no effect on segregation of the other two loci.

The data from the 17 inoculated progenies could be made to bear on the question of linkage between the *I/i* and cauliflower loci by breaking down each of the six categories of table 3 into two components based on whether or not Fusarium

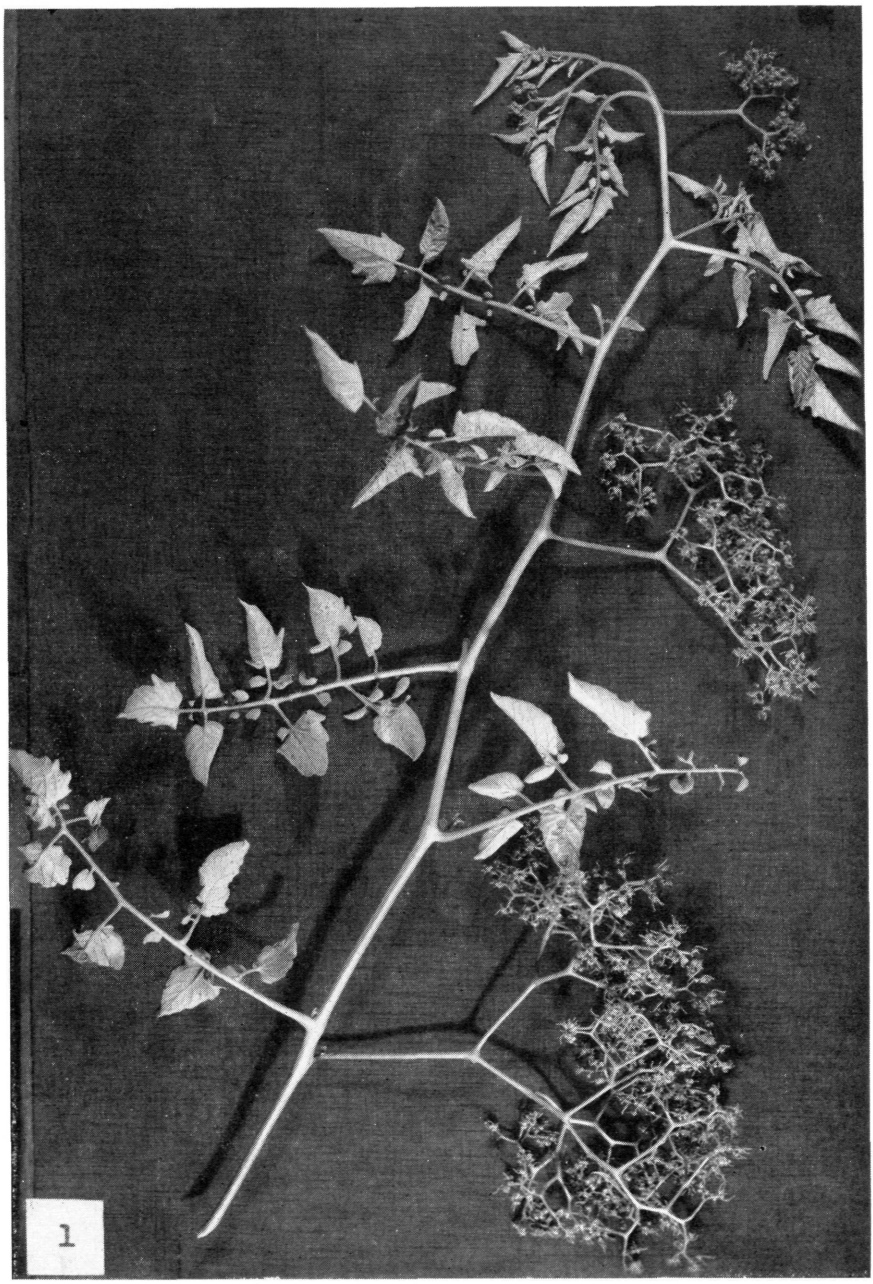

FIGURE 1. Branch from a cauliflower tomato plant. Every inflorescence is of the cauliflower type. × ca ⅓.

FIGURE 2. Histological section of a cauliflower type tomato inflorescence primordium. The growing points are not enclosed by leaf or scale primordia. One filiform bract primordium is visible above left center. × ca 50. (Preparation by Elizabeth Leeper.)

FIGURE 3. Portion of a cauliflower type inflorescence on which normal leafy stem growth has resumed. Inflorescences on this new growth continue to be of the cauliflower type. At each younger bifurcation, a subtending filiform bract is present. × ca 1.

FIGURE 4. Complex (*ss* genotype) inflorescence resembles cauliflower but has flowers. The two are not allelic. × ca ½.


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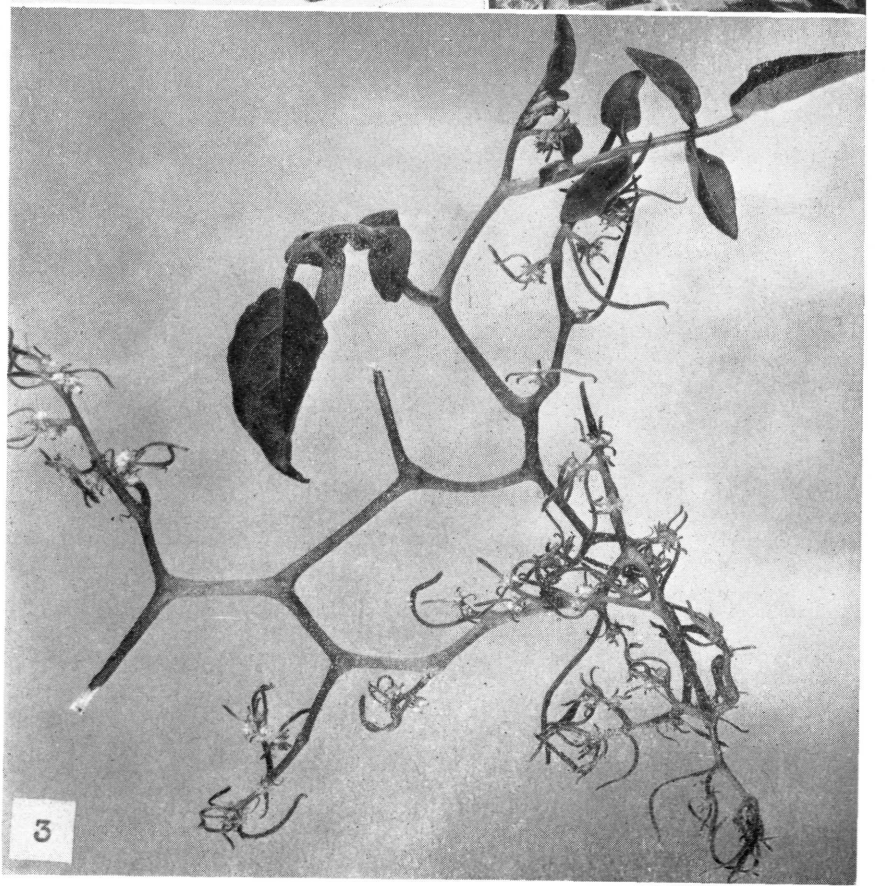
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TABLE 3

Frequency of 6 possible combinations of cauliflower genotype with stem hairiness genotype among 30 F_2 individuals as determined by F_3 progeny tests.

		No Cauliflower in F_3			Cauliflower in F_3					
		None hairy in F_3 (*HH*)	Some hairy in F_3 (*Hh*)	All hairy in F_3 (*hh*)	None hairy in F_3 (*HH*)	Some hairy in F_3 (*Hh*)	All hairy in F_3 (*hh*)	χ^2	df	P
17 Fusarium inoculated F_3 progenies		1	2	2	4	6	2	1.108	5	0.98–0.95
13 uninoculated F_3 progenies		3	4	1	0	5	0	8.943	5	0.20–0.10
Totals	Observed	4	6	3	4	11	2	3.300	5	0.70–0.50
	Expected	2.5	5.0	2.5	5.0	10.0	5.0			
Heterogeneity $\chi^2 = 6.751$; df = 5; P = 0.30–0.20										

TABLE 4

Frequency of 4 possible combinations of cauliflower genotype with Fusarium reaction genotype among 17 F_2 individuals as determined by subjecting their F_3 progeny to Fusarium inoculation.

	No Cauliflower in F_3		Some Cauliflower in F_3				
	All survived in F_3 (*II*)	Some did not survive in F_3 (*Ii*)	All survived in F_3 (*II*)	Some did not survive in F_3 (*Ii*)	χ^2	df	P
Observed	3	2	4	8	1.583	3	0.70–0.50
Expected	1.9	3.8	3.8	7.5			

susceptible individuals were present in the respective F_3 progenies. However, when this is done, the frequency in each class becomes too low to justify the use of the χ^2 method of analysis. This criticism actually applies already to the data of table 3. These data are therefore presented in table 4 in a manner that disregards the stem hairiness genotype. The deviation from a 1: 2: 2: 4 ratio is not significant, hence, apparently the cauliflower and *I*/*i* loci are not linked. On the basis of other hybridizations, and without knowledge of the work of Butler (1951), Paddock (1950) tentatively assigned the *I*/*i* locus to linkage group 5.

In the F_4 generation, 33 progenies were raised in the greenhouse during fall without Fusarium inoculation. Their parents include all the non-cauliflower members of two segregating F_3 progenies. Again it was expected that some cauliflower plants would appear in approximately two-thirds of these progenies and that in each such segregating progeny approximately one-fourth of the plants would have the cauliflower character. The two-thirds expectation was realized exactly (table 1) with 22/33 progenies segregating. Deviation from the one-fourth expectation is not significant (table 2).

F_5 generation data have been completed in the greenhouse during winter from seven F_4 individuals, all being non-cauliflower members of a single segregating F_4 progeny. None of the seven were subjected to Fusarium inoculation in F_5 generation. Among the seven progenies, five segregated (table 2). χ^2 for this deviation from a 2: 1 expectation is only 0.700 and P is 0.50–0.30 with 1 degree of freedom. The heterogeneity χ^2 for the ratios 5 : 8, 12 : 5, 22 : 11, and 5 : 2 is 4.736 with 3 degrees of freedom and P is 0.20–0.10. Therefore all 70 tested progenies may be treated as a single sample of 44 segregators to 26 non-segregators. The χ^2 for the deviation of 44 : 26 from the expected 2 : 1 is 0.4583 with 1 degree of freedom and P is 0.50–0.30.

The above F_4 progeny was chosen for F_5 study because all the cauliflower individuals in it had dwarfed inflorescences, while the non-cauliflower individuals had normal sized inflorescences. The dwarfing affected only the inflorescences. Such dwarfed cauliflower inflorescences had been noted from time to time in preceding generations on individual glasshouse raised plants but never on field raised plants. Among the five segregating F_5 progenies, three produced only the dwarfed form of the cauliflower inflorescence. In the other two progenies, there was only one individual in each progeny with the usual large form of cauliflower inflorescence. These facts indicate the existence of modifier genes which apparently are effective only when the plants are raised under glass. The matter is being investigated further.

Twelve progenies from six reciprocal hybridizations among five known cauliflower heterozygotes have been studied. The five parent individuals included three representatives from the F_4, one from the F_3, and one from the F_2. Each of the latter two was hybridized reciprocally with each of the former three. In each of the 12 progenies, the deviation from a 3: 1 expectation is not significant. The totals of all 12 progenies are in table 2.

The above two known cauliflower heterozygotes of F_2 and F_3 were also crossed reciprocally with MacArthur strain 706, as ovule parent with MacArthur strain 902, and as ovule parent with our woolly selection from P. A. Young strain G1075. From the reciprocal crosses, 13 plants among 18 had some cauliflower offspring after selfing. From the crosses with MacArthur strain 902, two plants among six had some. From the crosses with our woolly selection, 14 among 26 had some. In each of the three crosses, the deviation from a 1: 1 expectation is not significant. Their heterogeneity χ^2 is 2.002 with 2 degrees of freedom and P is 0.50–0.30. It is therefore permissible to treat all 50 progenies as a single sample of 29 segregators to 21 non-segregators. The χ^2 for the deviation of 29: 21 from the expected 1: 1 is 1.280 with 1 degree of freedom and P is 0.30–0.20. These 50 progenies qualify as F_2 repulsion tests of linkage. Discussion of their bearing on the linkage relation-

ships of the cauliflower locus will, however, be deferred until data can be acquired from back-crosses as well.

The crosses with MacArthur strain 706 are also a test for allelism between the cauliflower and complex (*S/s*) loci. Since neither cauliflower nor complex appeared in any of the 156 offspring observed, it is concluded the genes governing these two characters are not allelic. The writers, therefore, propose the symbol *ca* for the gene governing the cauliflower character.

There is considerable remnant seed on hand from progeny test identified *Ca/ca* plants. A sample will gladly be sent upon request.

SUMMARY

A new apparently mendelian recessive character, here proposed to be known as cauliflower and symbolized by *ca*, has been studied in four successive generations. There is no apparent linkage of the cauliflower locus with either the Fusarium immunity locus (*I/i*, probably group 5) or the stem hairiness locus (*H/h*, group 7). The cauliflower locus and the complex locus (*S/s*) are not allelic. There is some indication of the existence of modifier genes causing a dwarfed form of cauliflower.

LITERATURE CITED

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